# Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef

TIMOTHY F. COOPER\*†, GLENN DE'ATH\*, KATHARINA E. FABRICIUS\* and JANICE M. LOUGH\*

\*Australian Institute of Marine Science, PMB 3 Townsville MC, Townsville, Queensland 4810, Australia, †School of Marine and Tropical Biology, and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4810, Australia

## **Abstract**

Temporal and spatial variation in the growth parameters skeletal density, linear extension and calcification rate in massive Porites from two nearshore regions of the northern Great Barrier Reef (GBR) were examined over a 16-year study period. Calcification rates in massive *Porites* have declined by approximately 21% in two regions on the GBR  $\sim$  450 km apart. This is a function primarily of a decrease in linear extension ( $\sim$  16%) with a smaller decline in skeletal density ( $\sim$ 6%) and contrasts with previous studies on the environmental controls on growth of massive Porites on the GBR. Changes in the growth parameters were linear over time. Averaged across colonies, skeletal density declined over time from  $1.32 \,\mathrm{g \, cm^{-3}}$  (SE = 0.017) in 1988 to  $1.25 \,\mathrm{g \, cm^{-3}}$  (0.013) in 2003, equivalent to 0.36% yr<sup>-1</sup> (0.13). Annual extension declined from 1.52 cm yr<sup>-1</sup> (0.035) to  $1.28 \,\mathrm{cm} \,\mathrm{yr}^{-1}$  (0.026), equivalent to  $1.02\% \,\mathrm{yr}^{-1}$  (0.39). Calcification rates (the product of skeletal density and annual extension) declined from 1.96 g cm<sup>-2</sup> yr<sup>-1</sup> (0.049) to  $1.59 \,\mathrm{g\,cm^{-2}\,yr^{-1}}$  (0.041), equivalent to  $1.29\% \,\mathrm{yr^{-1}}$  (0.30). Mean annual seawater temperatures had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at  $\sim$ 26.7 °C. There were minor differences in the growth parameters between regions. A decline in coral calcification of this magnitude with increasing seawater temperatures is unprecedented in recent centuries based on analysis of growth records from long cores of massive Porites. We discuss the decline in calcification within the context of known environmental controls on coral growth. Although our findings are consistent with studies of the synergistic effect of elevated seawater temperatures and  $pCO_2$  on coral calcification, we conclude that further data on seawater chemistry of the GBR are required to better understand the links between environmental change and effects on coral growth.

Keywords: calcification, climate change, Great Barrier Reef

Received 27 April 2007; revised version received 4 October 2007 and accepted 2 November 2007

# Introduction

Massive corals record an environmental history in their calcium carbonate skeletons (Dodge & Vaisnys, 1975). They grow by precipitating calcium carbonate on previously deposited skeleton thereby creating a series of growth bands. The annual nature of the growth bands is well understood (Knutson *et al.*, 1972) as are other

Correspondence: Timothy F. Cooper, Australian Institute of Marine Science, PMB 3 Townsville MC, Townsville, QLD 4810, Australia, tel. +61 7 4753 4444, fax +61 7 4772 5852, e-mail: t.cooper@aims.gov.au

characteristics, including environmental effects on isotopic composition (Gagan *et al.*, 2000; McCulloch *et al.*, 2003), luminescence (Isdale, 1984), and the growth parameters skeletal density, annual extension and calcification rate (Barnes & Lough, 1989). Massive corals of the genus *Porites* are long lived, and distributed widely throughout the Indo-Pacific Ocean, across a range of habitats from turbid inshore to clear offshore waters. Their skeletal records are, therefore, eminently useful as a tool for detecting long-term changes in environmental conditions in tropical ocean surface waters.

Environmental controls on the growth of scleractinian corals include seawater temperature (Jokiel & Coles,

1978; Highsmith, 1979; Crossland, 1984; Lough & Barnes, 2000), light (Goreau & Goreau, 1959; Bak, 1974; Yentsch et al., 2002), carbonate saturation state (Marubini et al., 2001), water motion (Scoffin et al., 1992; Lesser et al., 1994), and water quality (Marubini & Davies, 1996; Fabricius, 2005). Recent attention has focused on the effects of rising concentrations of atmospheric greenhouse gases due to human activities on corals and coral reefs (Hughes et al., 2003; Lesser, 2004). Rising concentrations of atmospheric greenhouse gases (IPCC, 2001, 2007) have been associated with warming of the tropical oceans, resulting in an increased frequency of mass coral bleaching events since the 1970s (Hoegh-Guldberg, 2005). Concentrations of the principle greenhouse gas  $CO_2$  have risen  $\sim 35\%$  in the atmosphere since the late 18th century, presently increasing at about 1% annually. The current concentration of ~379 ppm in 2005 (WMO Greenhouse Gas Bulletin, 2006) is considered to be unprecedented in at least the past 650 000 years (Petit et al., 1999; Siegenthaler et al., 2005). High atmospheric CO<sub>2</sub> leads to increased concentrations of dissolved CO2 in seawater shifting the seawater carbonate equilibrium towards higher levels of bicarbonate (HCO<sub>3</sub><sup>-</sup>) by  $CO_{2(aq)} + H_2O + CO_3^{2-} \leftrightarrow$ 2HCO<sub>3</sub>. The dissolution of CO<sub>2</sub> reduces pH in ocean surface waters, lowers the availability of carbonate  $(CO_3^{2-})$  ions and decreases the calcium carbonate saturation state  $(\Omega)$ , a process called ocean acidification (e.g. Caldeira & Wickett, 2003). Aragonite saturation is predicted to decrease by around 30% by 2050, which is expected to have negative consequences on the growth rates of a range of calcifying biota (Kleypas et al., 1999; Feely et al., 2004; Orr et al., 2005). Although evidence from laboratory experiments has confirmed decreases in calcification rates with reduced aragonite saturation (Gattuso et al., 1998; Langdon et al., 2000; Leclercq et al., 2000; Schneider & Erez, 2006), data from field studies showing long-term declines in coral calcification rates are lacking (Kleypas et al., 1999). The aim of this study was to examine temporal and spatial variation in the growth parameters skeletal density, linear extension and calcification rate in massive Porites from two nearshore regions of the Great Barrier Reef (GBR), and to interpret these data in the context of changing environmental conditions.

#### Materials and methods

Study sites and sampling design

To examine spatial and temporal variation in the coral growth parameters skeletal density, annual extension and calcification rate, we collected 10 colonies of massive *Porites* at each of two coral reefs within each of two

regions (Far Northern and Northern, ~450 km apart; Fig. 1) on the GBR, Australia, in January 2004. In the Far Northern Region, colonies were collected from fringing reefs at Hannah (13°52'S, 143°43'E) and Hay Islands (13°40'S, 143°41'E), and in the Northern Region from High (17°10'S, 146°00'E) and Kent Islands (17°40'S, 146°11′E). The four reefs are located in the coastal zone (i.e. within the 20 m isobath) of the GBR lagoon (Alongi & McKinnon, 2005). Mean annual sea-surface temperature (SST) is  $\sim 0.5$  °C higher in the Far Northern than in the Northern Region (Rayner et al., 2003). All colonies were >30 cm in diameter and were collected from the leeward side of the islands at shallow depths (1-3 m below lowest astronomical tide). In total, 40 colonies were collected during the study but two colonies were excluded due to severe internal bioerosion, leaving a total of 38 colonies for the analysis of growth parameters.

# Sclerochronology

The growth parameters skeletal density, annual extension and calcification rate were determined for each colony following procedures described previously (Barnes & Lough, 1989; Chalker & Barnes, 1990; Lough & Barnes, 1990a, b). A slice ( $\sim$ 7 mm thick) was cut from the centre of each colony using a large saw with freshwater applied as lubricant, and dried for 12h at 60 °C. Each slice was then X-rayed using Kodak lanex regular, double-sided emulsion (100 mA, 0.032 s, 45 kV, 150 FFD; Rochester, NY, USA; Supplementary Fig. 1a). The positive X-ray prints were then used to identify two tracks on each colony with clear annual density bands avoiding convolutions in coral growth and bore holes from bioeroders (Lough et al., 1999). Along these tracks, skeletal density was determined with a y densitometer at 0.25 mm intervals. The X-ray prints were also used to date the annual growth bands based on the assumption that skeleton of greatest density is deposited in summer (Lough & Barnes, 1990a). Once each growth band was dated, it was possible to calculate (i) mean annual skeletal density as the average density between adjacent annual density minima (g cm<sup>-3</sup>); (ii) mean annual extension rate as the linear distance between adjacent annual density minima (cm yr<sup>-1</sup>); and (iii) mean annual rate of calcification (g cm<sup>-2</sup> yr<sup>-1</sup>) as the product of skeletal density and annual extension. The three variables were then averaged across the corresponding growth year from the two densitometer tracks (Lough & Barnes, 2000).

SST

SST were obtained for the 1° latitude by longitude box closest to the study locations [centred on 13.5°S, 143.5°E

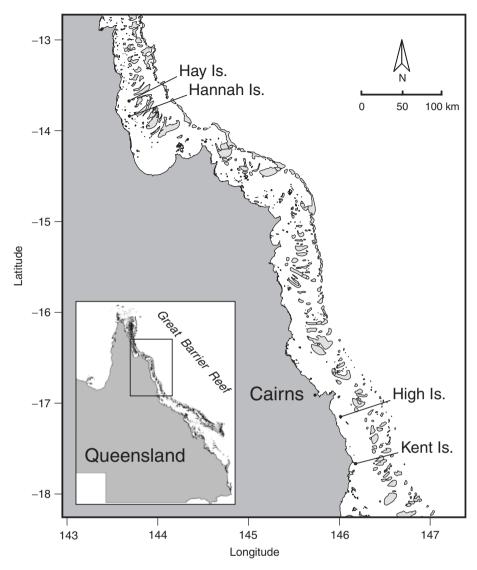


Fig. 1 Map of the Great Barrier Reef, and the reefs for collection of massive Porites colonies. Hay and Hannah Islands are in the Far Northern Region, High and Kent Island in the Northern Region of the Great Barrier Reef.

for the Far Northern and 17.5°S, 146.5°E for the Northern GBR, Supplementary material Fig. S1(b)] for 1971-2003 from the global HadISST 1.1 database (http:// www.badc.nerc.ac.uk/data/HadISST/) (Rayner et al., 2003). Average annual SST corresponding (approximately) to the coral growth years was calculated as arithmetic means of the average monthly values for each box.

# Statistical analyses

The statistical analyses investigated how the growth variables (skeletal density, annual extension and calcification rate) varied with year, SST and reef. The age of the annual growth bands in the colonies ranged from

1971 to 2003 [Supplementary material Fig. S1(c)], but there were few bands recorded before 1988, and hence the data selected for analysis focused on the 16-year period from 1988 to 2003. Thus, the data obtained from the 38 colonies were unevenly distributed across years and reefs (Table 1).

The data comprised repeated measures across years on colonies. Such measures are likely to be correlated for individual colonies (Lough & Barnes, 1997), and exploratory data analysis suggested this to be the case (Fig. 2). This correlation was modelled by fitting profiles over time for each of the colonies as part of linear-mixed models analyses (Laird & Ware, 1982; Pinheiro & Bates, 2000). These models comprise fixed and random effects, and a hierarchy of models was explored as follows. For

**Table 1** The numbers of colonies observed by (a) year and (b) reef shows the imbalance in the data due to fewer colonies having bands in earlier years

(a)								
Year	1988	1989	1990	1991	1992	1993	1994	1995
n	14	17	19	21	24	28	33	35
Year	1996	1997	1998	1999	2000	2001	2002	2003
n	36	37	38	38	38	38	38	38

(b)				
Reef	Hannah	Hay	High	Kent
n	9	9	10	10

each response, a saturated fixed model was selected initially, and was adequately complex to include all effects of interest. It contained smooth trends over years (natural splines, df = 4), smooth effects in SST (natural splines, df = 4), reef effects and all first-order interactions between these terms. The random components of the model were then selected based on the Akaike Information Criterion (AIC) with the model fitted by restricted maximum likelihood estimation (Pinheiro & Bates, 2000). This involves calculation of AIC for all models of interest and then choosing the one with the minimum AIC. The random effects considered included combinations of (1) smooth profiles across years (natural splines, df = 3), (2) linear profiles over years and (3) random intercepts for each coral. The random effects selected were: (1) for skeletal density, linear trends in years with additive effects of colonies, and (2) for annual extension and calcification rate, only effects of colonies. Once the random structure was selected, the fixed components of the model were assessed for each response. A preliminary analysis showed interactions to be negligible, and only main effects were considered thereafter. For each response, the degree of smoothness for terms involving years and SST were estimated by cross validation (Wood, 2006). The estimates are documented in Table 2. All analyses were done using the statistical program R (R Development Core Team, 2006).

#### **Results**

There was significant variation in all three growth parameters among the 38 *Porites* colonies over the period 1988–2003 (Fig. 2). When averaged across colonies, skeletal density declined over time from  $1.32\,\mathrm{g\,cm^{-3}}$  (SE = 0.017) in 1988 to  $1.25\,\mathrm{g\,cm^{-3}}$  (0.013) in 2003, an average annual decline of 0.00475 g cm<sup>-3</sup> (0.0017) or  $0.36\%\,\mathrm{yr^{-1}}$  (0.13) (Fig. 3a). Annual extension declined from  $1.52\,\mathrm{cm\,yr^{-1}}$  (0.035) to  $1.28\,\mathrm{cm\,yr^{-1}}$  (0.026)

[i.e.  $0.0133\,\mathrm{cm\,yr^{-1}}$  (0.0039) or  $1.02\%\,\mathrm{yr^{-1}}$  (0.39)]. Consequently, calcification rate declined from  $1.96\,\mathrm{g\,cm^{-2}\,yr^{-1}}$  (0.049) to  $1.59\,\mathrm{g\,cm^{-2}\,yr^{-1}}$  (0.041), equivalent to an annual decline of  $0.0243\,\mathrm{g\,cm^{-2}\,yr^{-1}}$  (0.0051) or  $1.29\%\,\mathrm{yr^{-1}}$  (0.30). SST had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at  $\sim\!26.7\,^{\circ}\mathrm{C}$  (Fig. 3b). At higher and lower temperatures both parameters declined by  $\sim\!15\%\,\mathrm{per}\,^{\circ}\mathrm{C}$ . Differences in coral growth parameters across the four reefs were small when adjusted for temporal trends and regional differences in SST, with marginally lower extension and calcification rates on the two northern reefs compared with the far northern reefs (Fig. 3c).

# Discussion

This study has shown that calcification rates in massive Porites in two nearshore regions ~450 km apart on the GBR have declined by 21% over a 16-year study period between 1988-2003. A range of environmental factors known to influence coral growth may have contributed to this decline. Seawater temperature is an important environmental factor controlling coral growth (Highsmith, 1979; Crossland, 1984; Lough & Barnes, 2000). Several laboratory studies have found nonlinear responses in calcification to temperature, with a peak around 25-26 °C and decreasing beyond this range (Jokiel & Coles, 1978; Marshall & Clode, 2004). Our finding of a modal response in coral calcification to SST, with maxima at 26.7 °C, suggests a thermal optimum in calcification may occur around this SST also in the field. A previous study has shown that along a latitudinal gradient, long-term average growth rates in Porites were related linearly to long-term mean annual SST, with each 1°C increase in SST corresponding to an increase of  $0.39 \,\mathrm{g \, cm^{-2} \, yr^{-1}}$  in calcification and  $3.1 \,\mathrm{mm \, yr^{-1}}$  in annual extension (Lough & Barnes, 2000). The results of that study are not strictly comparable with our results

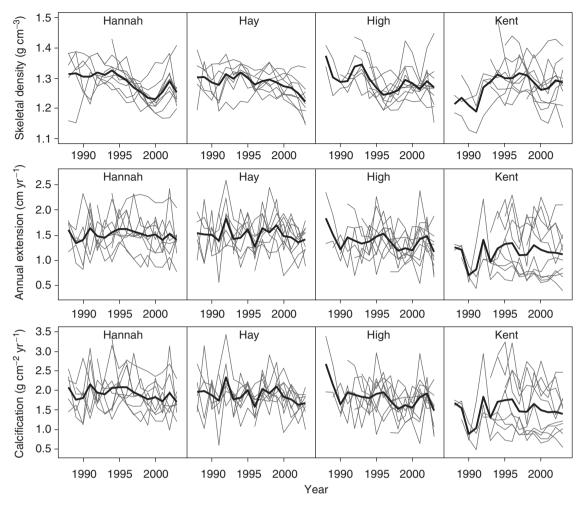


Fig. 2 Temporal profiles for skeletal density, annual extension and calcification rate over years. The grey lines indicate individual corals and the black lines indicate the mean profiles. The variation of annual extension and calcification are large (coefficient of variation, CV = 30.5% and 30.3%, respectively) compared with skeletal density (CV = 9.1%).

since we estimated effects of SST after adjusting for reef (hence latitudinal) effects and temporal trends. However, our finding of a nonlinear relationship of coral growth and temperature adds further evidence to recent arguments (Kleypas et al., 2005) rebutting a prediction of  $\sim 35\%$  increase in coral calcification beyond preindustrial levels due to warming oceans (McNeil et al., 2004).

Thermal stress is also an important environmental control on coral growth, occurring with increasing frequency and intensity within recent decades. Increases in SST above the upper thermal limit of corals can have negative physiological consequences on coral energetic reserves (Anthony et al., 2007) and tissue biomass (Fitt et al., 2000). Further, Suzuki et al. (2003) found that calcification of massive Porites from the GBR declined following the 1998 bleaching event. Mean monthly SST maxima for the Northern and Far North-

Table 2 Cross-validated estimates of smoothness (degrees of freedom) of trends in years and sea-surface temperature for skeletal density, annual extension and calcification.

Model terms	Skeletal de	ensity Annual ext	ension Calcification		
Years	3.00	1.20	1.39		
Sea-surface	1.00	3.58	3.11		
temperature					

Estimates were based on linear mixed effects models.

ern Region are 28.87 and 29.13 °C, respectively, for the period 1900-2003 (HadISST dataset). The cumulative number of degree heating months, an index of thermal stress and an extension of the degree heating week indicator (Liu et al., 2003), was 1.33 in the Northern Region in both 1998 and 2002, and 1.06 and 0.88 in the Far Northern Region. Indeed, nearshore reefs in our

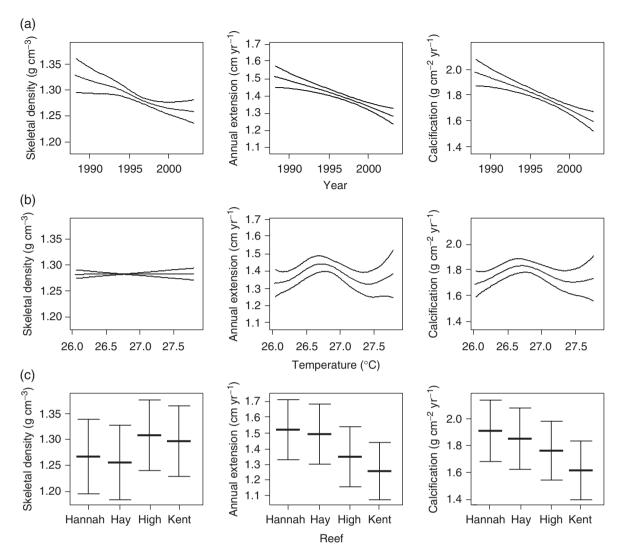


Fig. 3 Partial effects plots showing the estimated dependencies (with 95% confidence intervals) of skeletal density, annual extension and calcification on (a) year, (b) sea surface temperature and (c) reef. Hannah and Hay Island are in the Far Northern Region, High and Kent in the Northern Region of the Great Barrier Reef. Each partial effects plot is adjusted for the effects of the other two explanatory variables.

Northern study area experienced severe (>60% bleached coral cover) bleaching in 1998 and moderate (1–30%) bleaching in 2002 (Berkelmans *et al.*, 2004). Our Far Northern Region was not surveyed in 1998 but experienced major bleaching (i.e. 30–60%) in 2002. Thus, an increasing frequency in thermal stress may in part explain the observed decline in calcification of *Porites* colonies in the northern GBR.

A range of other environmental factors are also known to affect coral growth in particular light and turbidity (Barnes & Chalker, 1990). While the growth parameters in shallow-water massive *Porites* (n = 245) along a 9° latitudinal gradient on the GBR were unrelated to surface irradiance (Lough & Barnes, 2000),

linear extension in four species of massive corals decreased along a light gradient from 1 to 30 m water depth (Huston, 1985). Similarly, skeletal density and calcification rate in the coral *Montastraea annularis* increased with decreasing turbidity and sedimentation, while linear extension decreased (Carricart-Ganivet & Merino, 2001) although this may have been a growth response to increasing SST (Carricart-Ganivet, 2004). Wave energy is also an important environmental factor influencing coral growth. Colonies growing in wave-exposed conditions have greater skeletal density and lower linear extension compared with those protected from wave action (Scoffin *et al.*, 1992). In our study, all colonies were sampled on the leeward side of continen-

tal islands. As light, turbidity and waves vary spatially in relation to sediment resuspension by wind on the GBR (Larcombe et al., 1995; Orpin et al., 2004), these factors may have contributed to the marginal differences in coral growth between the four reefs. Dissolved inorganic nutrients and sedimentation can also have negative effects on coral growth (e.g. Ferrier-Pages et al., 2000 and review by Fabricius, 2005). In the Northern Region, land use in catchments has intensified over the last 150 years (predominantly for cattle grazing, and sugarcane and banana cropping, Furnas, 2003). In contrast, the Far Northern Region is sparsely populated, has no cropping and only localized low-density cattle grazing, and hence the amount of pollutants in terrestrial runoff is low compared with the Northern Region (Brodie et al., 2007). Levels of nutrients and turbidity in reef waters are indeed substantially lower in the Far Northern than in the Northern Region (Fabricius & De'ath, 2004). However, the coral growth parameters of this study showed only minor differences between regions after controlling for temperature effects. The observed temporal decline in coral growth in both regions is, therefore, not consistent with changing water quality.

Large-scale interdecadal changes in seawater chemistry may also potentially explain the decline in coral calcification. Currently, the surface waters on coral reefs are supersaturated with the calcium carbonate minerals aragonite and calcite. Given that calcification rates of marine biota are proportional to the saturation state of calcium carbonate, the predicted decline in the saturation of aragonite under various climate change scenarios is cause for considerable concern (Smith & Buddemeier, 1992; Feely et al., 2004). For example, Kleypas et al. (1999) estimated that aragonite saturation state ( $\Omega_{arag}$ ) had decreased from preindustrial levels of  $4.6 \pm 0.2$  to current levels of  $4.0 \pm 0.2$ . A further study by Kleypas & Langdon (2002) estimated that the doubling of atmospheric pCO2 by 2065 would result in a decrease in the concentrations of seawater  $CO_3^{2-}$ of  $\sim$ 35%. Similarly, Orr et al. (2005) predicted that the upper ocean layers at high latitudes would become undersaturated with aragonite by 2050 and further suggested that current carbonate concentrations in tropical surface waters had already declined by  $29 \,\mu\text{mol kg}^{-1}$  (~10%) compared with preindustrial levels.

Recognizing that carbonate chemistry is a key determinant of calcification rates in corals, a number of experiments have reported the effects of manipulating aragonite saturation, pH and pCO<sub>2</sub> on coral growth (Gattuso et al., 1998; Marubini & Atkinson, 1999; Langdon et al., 2000; Leclercq et al., 2000; Marubini et al., 2001). For example, Langdon et al. (2000) found a 12-fold increase in coral calcification corresponding to a 55% increase in  $CO_3^{2-}$  concentration, while Leclercq et al. (2000) also reported linear declines with  $\sim 30\%$ decrease in calcification when aragonite saturation decreased from  $\Omega_{arag}$  5.4 to 1.3 as a function of increasing pCO<sub>2</sub>. Similarly, Schneider & Erez (2006) found that a  $\sim 30\%$  decrease in  $CO_3^{2-}$  concentration resulted in a  $\sim$ 50% decline in calcification in *Acropora eurystoma*. These and other studies show that lowering aragonite saturation, as a function of increasing concentrations of atmospheric CO<sub>2</sub>, can lead to declines in coral growth.

A 300-year coral core showed that pH varied naturally by 0.3 pH units over ~50-year cycles in the semienclosed lagoon of Flinders Reef (located in oceanic waters 150 km off the GBR in the Coral Sea), which was interpreted in the context of interdecadal climate variability influencing lagoonal flushing by trade winds (Pelejero et al., 2005). Contrary to results from laboratory experiments, the variation in aragonite saturation and pH within the lagoon of Flinders Reef had no apparent effect on calcification in this coral (Pelejero et al., 2005). However, the reconstruction is based on a single coral core in a semienclosed environment, thus limiting generalizations about effects of variations in seawater pH on calcification and on processes in more open regions like the GBR. Indeed, the variation among the temporal profiles of our individual colonies suggests that the observed changes in calcification may not have been detected without the substantial number of colony replicates used in this study.

It is not possible to determine whether the observed decline in calcification was due to changes in seawater chemistry because data on aragonite saturation for the GBR are lacking. However, the atmospheric concentration of CO<sub>2</sub> at Mauna Loa, Hawaii, was 351.44 ppm in 1988 increasing to 375.61 ppm in 2003 (Keeling & Whorf, 2005) representing an increase of 6.4%  $(0.40\% \, \mathrm{yr}^{-1})$  over the study period. Assuming a  $\Omega_{\mathrm{arag}}$ of 4.0 in 2003 (Kleypas et al., 1999), the increase in atmospheric  $CO_2$  corresponds to an approximate  $\Omega_{arag}$ of 4.26 in 1988, equivalent to a 6.1% decline in saturation. Experimental evidence suggests the relationship between coral calcification and aragonite saturation is linear (Marubini & Thake, 1999; Langdon et al., 2000; Leclercq et al., 2000; Schneider & Erez, 2006) although some have reported nonlinear responses (Gattuso et al., 1998; Ohde & van Woesik, 1999). Nevertheless, the 21% decline in coral calcification presented here is 3.5-fold greater than is predicted from laboratory studies. The discrepancy between our results and the laboratory and mesocosm studies suggests the existence of some other factors or synergistic mechanisms contributing to the observed decline in coral growth.

Growth records from long cores of massive Porites showed that mean calcification was  $\sim 4\%$  higher in the 50-year period from 1930 to 1979 compared with the previous 50 years (i.e. 1880-1929, Lough & Barnes, 1997). It was suggested that calcification in some corals might, at least initially, increase with rising SST (Lough & Barnes, 2000; Carricart-Ganivet, 2004) and air temperature (Bessat & Buigues, 2001). Up to 1982, there was no evidence of a size or age-dependent decline in calcification rates in long cores spanning several centuries of growth (Lough & Barnes, 1997). We found a decrease in calcification for the subsequent period between 1988 until 2003, despite a concurrent average SST increase of  $0.024 \pm 0.017$  °C yr<sup>-1</sup> on the GBR. This suggests that calcification rates in massive corals have decreased in response to changing environmental conditions since the studies by Lough & Barnes (1997, 2000) were completed.

The synergistic effects of elevated seawater temperatures and changing seawater chemistry on coral phyonly recently have gained attention. Calcification in Stylophora pistillata declined by 50% in experimental treatments of elevated seawater temperatures and pCO<sub>2</sub> (Reynaud et al., 2003). The long-term effects of the increasing frequency of mass bleaching events, coupled with changing seawater chemistry, on the growth rates of corals on the GBR are poorly understood, but the results of Reynaud et al. (2003) provide some insight to the patterns of decline reported here. A recent study suggested that coral calcification should have started declining due to a lowering of aragonite saturation (Kleypas et al., 1999). Here, it has not been possible to assess the observed decline in calcification rates in massive Porites in the context of changes in aragonite saturation state as these data are not available for the GBR. However, the existence of a 21% decline in coral calcification in the two study regions is of concern. Given the economic and ecological value of the GBR and other coral reefs around the world, the monitoring of pH and aragonite saturation, coupled with controlled experiments on synergistic effects of increasing SST and a range of water quality variables including aragonite saturation, are required to better understand the links between environmental change and their effects on coral growth.

# Acknowledgements

We thank Eric Matson and Damian Thomson for assistance in slicing and X-raying the corals, and Craig Humphrey for assistance in the field. An earlier version of the manuscript benefited from the constructive comments of three anonymous reviewers. This study was supported by joint contributions from the Australian Institute of Marine Science, and the Cooperative

Research Centre (CRC) for Coral Reefs and CRC Rainforest to the Catchment to Reef Program.

## References

- Alongi DM, McKinnon AD (2005) The cycling and fate of terrestrially-derived sediments and nutrients in the coastal zone of the Great Barrier Reef shelf. *Marine Pollution Bulletin*, **51**, 239–252.
- Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. *Limnology and Oceanography*, **52**, 716–726.
- Bak RPM (1974) Available light and other factors influencing growth of stony corals through the year in Curacaco. Proceedings of the second International Coral Reef Symposium, Brisbane, Australia, pp. 229–233.
- Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Ecosystems of the World 25, Coral Reefs (ed. Dubinsky Z), pp. 109–131. Elsevier, Amsterdam.
- Barnes DJ, Lough JM (1989) The nature of skeletal density banding in scleractinian corals: fine banding and seasonal patterns. *Journal of Experimental Marine Biology and Ecology*, **126**, 119–134.
- Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs*, 23, 74–83.
- Bessat F, Buigues D (2001) Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography Palaeoclimatology Palaeoe-cology*, 27, 1–12.
- Brodie J, De'ath G, Devlin MJ, Furnas MJ, Wright M (2007) Spatial and temporal trends of near-surface chlorophyll *a* in the Great Barrier Reef lagoon. *Marine and Freshwater Research*, **58**, 342–353, doi: 10.1071/MF06236.
- Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. *Nature*, **425**, 365–365.
- Carricart-Ganivet JP (2004) Sea surface temperature and the growth of the West Atlantic reef-building coral Montastraea annularis. Journal of Experimental Marine Biology and Ecology, 302, 249–260.
- Carricart-Ganivet JP, Merino M (2001) Growth responses of the reef-building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico. *Bulletin of Marine Science*, **68**, 133–146.
- Chalker BE, Barnes DJ (1990) Gamma densitometry for the measurement of skeletal density. *Coral Reefs*, **9**, 11–23.
- Crossland CJ (1984) Seasonal variations in the rates of calcification and productivity in the coral *Acropora formosa* on a high-latitude reef. *Marine Ecology Progress Series*, **15**, 135–140.
- Dodge RE, Vaisnys JR (1975) Hermatypic coral growth banding as environmental recorder. *Nature*, **258**, 706–708.
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.

- Fabricius KE, De'ath G (2004) Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications, 14. 1448-1465.
- Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO sub(2) on the CaCO sub(3) system in the oceans. Science, 305, 362-366.
- Ferrier-Pages C, Gattuso J-P, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral Stylophora pistillata. Coral Reefs, 19, 103-113.
- Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography, 45, 677-685.
- Furnas MJ (2003) Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science, CRC Reef, Townsville, Australia.
- Gagan MK, Avliffe LK, Beck JW, Cole JE, Druffel ERM, Dunbar RB, Schrag DP (2000) New views of tropical paleoclimates from corals. Quaternary Science Reviews, 19, 45-64.
- Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. Global and Planetary Change, 18, 11-2.
- Goreau TF, Goreau NI (1959) The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. Biological Bulletin (Woods Hole), 117, 239-259.
- Highsmith RC (1979) Coral growth rates and environmental control of density banding. Journal of Experimental Marine Biology and Ecology, 37, 105-125.
- Hoegh-Guldberg O (2005) Low coral cover in a high-CO<sub>2</sub> world. Journal of Geophysical Research, 110, C09S06, doi: 10.1029/ 2004JC002528.
- Hughes TP, Baird AH, Bellwood DR et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science, 301, 929-933.
- Huston M (1985) Variation in coral growth rates with depth at discovery Bay, Jamaica. Coral Reefs, 4, 19-25.
- IPCC (2001) In: Climate Change 2001 Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change (eds Watson RT, and the Core Writing Team). Cambridge University Press, Cambridge, UK, 398 pp.
- IPCC (2007) In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL). Cambridge University Press, Cambridge, UK,
- Isdale PJ (1984) Fluorescent bands in massive corals record centuries of coastal rainfall. Nature, 310, 578-579.
- Jokiel PL, Coles SL (1978) Effects of temperature on the mortality and growth of Hawaiian reef corals. Marine Biology, 43, 201-208.
- Keeling CD, Whorf TP (2005) Atmospheric CO<sub>2</sub> Records from Sites in the SIO Air Sampling Network, Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN, USA.

- Kleypas J, Buddemeier R, Archer D, Gattuso J-P, Langdon C, Opdyke B (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science, 284, 118-
- Kleypas JA, Buddemeier RW, Eakin CM et al. (2005) Comment on "coral reef calcification and climate change: the effect of ocean warming". Geophysical Research Letters, 32, L08601, doi: 10.1029/2004GL022329.
- Kleypas J, Langdon C (2002) Overview of CO sub(2)-induced changes in seawater chemistry. Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia, pp. 1085–1089.
- Knutson DW, Buddemeier RW, Smith SV (1972) Coral chronometers: seasonal growth bands in reef corals. Science, 177, 270-272.
- Laird NM, Ware JH (1982) Random-effects models for longitudinal data. Biometrics, 38, 963-974.
- Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J (2000) Effect of calcium carbonate saturation on the calcification rate of an experimental coral reef. Global Biogeochemical Cycles, 14, 639-654.
- Larcombe P, Ridd PV, Prytz A, Wilson B (1995) Factors controlling suspended sediment on inner-shelf coral reefs. Townsville, Australia. Coral Reefs, 14, 163-171.
- Leclercq N, Gattuso J-P, Jaubert J (2000) CO sub(2) partial pressure controls the calcification rate of a coral community. Global Change Biology, 6, 329-334.
- Lesser MP (2004) Experimental biology of coral reef ecosystems. Journal of Experimental Marine Biology and Ecology, 300. 217-252.
- Lesser MP, Weis VM, Patterson MR, Jokiel PL (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral, Pocillopora damicornis (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. Journal of Experimental Marine Biology and Ecology, 178, 153-179.
- Liu G, Strong AE, Skirving WJ (2003) Remote sensing of sea surface temperatures during 2002 barrier reef coral bleaching. EOS, Transactions, American Geophysical Union, 84, 137-144.
- Lough JM, Barnes DJ (1990a) Intra-annual timing of density band formation of Porites coral from the central Great Barrier Reef. Journal of Experimental Marine Biology and Ecology, 135,
- Lough JM, Barnes DJ (1990b) Measurement of density in slices of coral skeleton: effect of densitometer beam diameter. Journal of Experimental Marine Biology and Ecology, 143, 91-99.
- Lough JM, Barnes DJ (1997) Several centuries of variation in skeletal extension, density and calcification in massive Porites colonies from the great barrier reef: a proxy for seawater temperature and a background of variability against which to identify unnatural change. Journal of Experimental Marine Biology and Ecology, 211, 29-67.
- Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral Porites. Journal of Experimental Marine Biology and Ecology, 245, 225-243.
- Lough JM, Barnes DJ, Devereux MJ, Tobin BJ, Tobin S (1999) Variability in Growth Characteristics of Massive Porites on the Great Barrier Reef, CRC Reef Research Centre Technical Report No. 28. CRC Reef, Townsville, Australia.

- Marshall AT, Clode P (2004) Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. *Coral Reefs*, **23**, 218–224.
- Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Marine Ecology Progress Series*, **188**, 117–121.
- Marubini F, Barnett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Marine Ecology Progress Series*, **220**, 153–162.
- Marubini F, Davies PS (1996) Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Mar*ine Biology, 127, 319–328.
- Marubini F, Thake B (1999) Bicarbonate addition promotes coral growth. *Limnology and Oceanography*, **44**, 716–720.
- McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner great barrier reef since European settlement. *Nature*, **421**, 727–730.
- McNeil BI, Matear RJ, Barnes DJ (2004) Coral reef calcification and climate change: the effect of ocean warming. *Geophysical Research Letters*, **31**, L22309, doi: 10.1029/2004GL021541.
- Ohde S, van Woesik R (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bulletin of Marine Science*, **65**, 559–576.
- Orpin AR, Ridd PV, Thomas S, Anthony KRN, Marshall P, Oliver J (2004) Natural turbidity variability and weather forecasts in risk management of anthropogenic sediment discharge near sensitive environments. *Marine Pollution Bulletin*, 49, 602–612.
- Orr JC, Fabry VJ, Aumont O *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.
- Pelejero C, Calvo E, McCulloch MT, Marshall JF, Gagan MK, Lough JM, Opdyke BN (2005) Preindustrial to modern interdecadal variability in coral reef pH. Science, 309, 2204–2207.
- Petit JR, Jouzel J, Raynaud D *et al.* (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, **399**, 429–436.
- Pinheiro JC, Bates DM (2000) Mixed-Effects Models in S and S-Plus. Springer Verlag, New York.
- R Development Core Team (2006) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rayner NA, Parker DE, Horton EB et al. (2003) Global analyses of sea surface temperature, sea ice and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research*, 108, 4407, doi: 10.1029/2002JD002670.
- Reynaud S, Leclercq N, Romaine-Lioud S, Ferrier-Pages C, Jaubert J, Gattuso J-P (2003) Interacting effects of CO<sub>2</sub> partial

- pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biology*, **9**, 1660–1668.
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnology and Oceanography*, **51**, 1284–1293.
- Scoffin TP, Tudhope AW, Brown BE, Chansang H, Cheeney RF (1992) Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs*, **11**, 1–11.
- Siegenthaler U, Stocker TF, Monnin E et al. (2005) Stable carbon cycle-climate relationship during the late Pleistocene. Science, 310, 1313–1317.
- Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics*, **23**, 89–118.
- Suzuki A, Gagan MK, Fabricius KE, Isdale PJ, Yukino I, Kawahata H (2003) Skeletal isotope microprofiles of growth perturbations in Porites corals during the 1997–1998 mass bleaching event. *Coral Reefs*, **22**, 357–369.
- WMO Greenhouse Gas Bulletin (2006) The state of greenhouse gases in the atmosphere using global observations through 2005. www.wmo.ch/web/arep/gaw/ghg/ghgbull06.html
- Wood SN (2006) Generalized Additive Models: An Introduction With R. Chapman & Hall/CRC, Florida, USA.
- Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW (2002) Sunlight and water transparency: cornerstones in coral research. *Journal of Experimental Marine Biology and Ecology*, **268**, 171–183.

## Supplementary material

The following material is available for this article online:

- Fig. S1. (a) X-ray of a coral slice showing a 33-year growth record for a massive *Porites* from Kent Island in the Northern Region of the Great Barrier Reef, (b) mean annual sea surface temperature for the Northern Region over the same period and (c) calcification rate of the colony. Dashed lines are 95% confidence intervals.
- This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2486.2007.01520.x
- Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.